# GILL STRUCTURE IN THE CAECILIAN GENUS *GYMNOPIS*

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Dunn (1942) reported that gills are absent in *Gymnopis* and Cochran (1961:16) stated that gills are not known for members of the genus. Some indication of gills has been found in all other New World caecilian genera. *Rhinatrema* (Noble, 1927; Parker, 1934), *Siphonops* (Goeldi, 1899), *Chthonerpeton* (Parker and Wettstein, 1929; Parker, 1956; Parker and Dunn, 1964) and *Typhlonectes* (Peters, 1874, 1875; Sarasins, 1887-90) all have gilled embryos; slits, but not gills, have been reported in young *Caecilia* (Tschudi, 1845).

An adult female *Gymnopis multiplicata proxima* with oviducal embryos (CRE 132 in the University of Southern California Costa Rican collections) was collected at Zent, Limon Province, Costa Rica, on 5 May, 1958. The adult is 367 mm. total length, has 117 primary annuli, 98 secondary annuli, an invisible eye, a well ossified skull with the eye and tentacular groove roofed by bone, the normal adult dentition, and is dark grey dorsally with a cream colored venter (in preservation). The embryos were found to have triramous, filamented gills. Of the four embryos, all developing in the left oviduct, the posteriormost (53.5 mm. total length) has no gills; of two lying side by side anteriorly a 54-mm. specimen has the left gill in a normal position and the right held only by a long strand of connective tissue; the 45-mm. embryo beside it has well developed gills on both sides of the head; the anteriormost embryo (52 mm.) also has a pair of well developed gills. The embryos have 110 to 117 primary annuli, secondaries distinguishable only on the posterior quarter of the body, the eyes covered by skin but well pigmented, an open tentacular groove, larval teeth as described for the species by Taylor (1955) and Parker and Dunn (1964), and large melanophores scattered over an otherwise unpigmented skin. There is no sign of an egg membrane.

Two females collected at Los Diamantes, Limon Province, Costa Rica, 17 June, 1962, carried embryos 80 to 84 mm. in length. Two embryos lay in each oviduct of a 412-mm. female and three in the left, two in the right of a 430-mm. adult. The adults have 117 and 119 primary annuli and 99 and 100 secondary annuli respectively.

The embryos have 109 to 117 primary annuli and 90 to 96 secondary annuli, the eye and tentacular groove roofed, though the eye is still slightly visible, and a reduced number of deciduous teeth. Coloration is similar to that of the smaller embryos. Gills are not present in any of the Los Diamantes embryos.

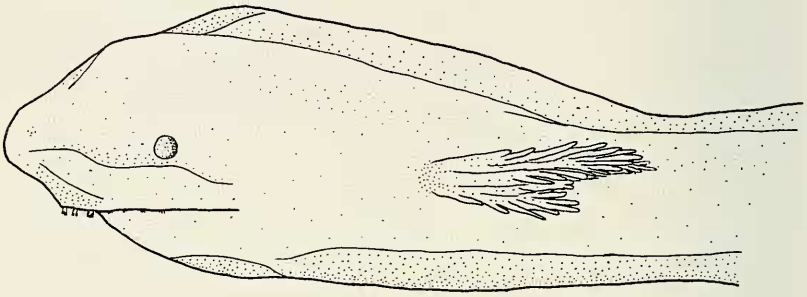

*Figure 1.* Left side of head and gills of 52-mm. *Gymnopis* embryo. 12 x. Line = 1 mm.

*External morphology of the gill*: The head and left gill of the 52-mm. specimen are shown in Figure 1. The gills originate 5.4 mm. from the anterior tip of the head and 2.0 mm. from the posterior end of the mouth. Measurements were made with a vernier caliper. The right gill has three fringed rami arising from a short stump attached to the head. The central ramus is nearly twice as long (3.7 mm.) as the upper and lower (2.0 mm. and 1.9 mm., respectively). The central ramus arises from a stout base (0.6 mm. wide and 0.5 mm. long). This ramus has four filaments (1.2 to 1.7 mm. long) at regular intervals along its lower side, a terminal tuft of three filaments (all 0.8 mm.) distally, and two filaments (1.1 and 1.2 mm.) on its upper side. The upper ramus bears four dorsal filaments (all 1.4 mm.), a terminal tuft of four filaments (0.6 to 0.7 mm.) and two ventral filaments (0.5 to 1.0 mm.). The lower ramus has two dorsal filaments (both 0.75 mm.); the terminal tuft is broadly united with short free filament ends (all 0.2 mm.); the ramus has four ventral filaments (all 1.0 mm.). The rami of the left gill measured 2.0 mm., 3.3 mm., and 1.8 mm., uppermost listed first. The upper ramus has three dorsal filaments (1.2 to 1.4 mm.), an end tuft of three filaments (0.5 to 0.7 mm.), and two ventral filaments (all 1.0 mm.). The central ramus has four dorsal filaments (1.2 to 1.8 mm.); the terminal group of filaments is somewhat united with three free ends (all 0.5 mm.); there are four ventral filaments (1.2 to 1.6 mm.). The

lower ramus has two dorsal filaments (0.75 to 1.2 mm.), four end filaments broadly united with short free ends (all 0.2 mm.), and three ventral filaments (all 1.0 mm.). Neither side has an open gill slit.

*Microscopic anatomy of the gill*: Serial sections of the head and gill area of the 54-mm. embryo were made and stained with Azan or hematoxylin-eosin by standard procedures. The gills at the stage of development examined are little more than sinuses containing red blood cells. Together with the tissue structure, the sinusoidal nature of the gills indicates degeneration of the structure and imminent loss. There is neither cartilaginous nor bony gill support, though a ventrally located hyobranchial apparatus is present. Fibrous connective tissue follows the epithelial layer only into the base of the gill (see Fig. 2). The gill ramus is formed by a stratified epithelial layer one or two cells thick; the layer is continuous with the epithelium of the head. The central part of each ramus is a vacuity filled with red blood cells. The filaments are formed by outpocketings of the epithelial layer. Several of the filaments close to the base of each ramus are also hollow and contain red blood cells; those smaller or further away are usually solid epithelial tissue. The ventral side of some rami and the filaments of the terminal tuft have a peripheral third layer of free-ended columnar epithelial cells. Three arterial arches pass through the base of the gill and are contained within the connective tissue of the head. These do not have channels into the rami, but pockets in the outer layer of the arch and the curve of the vessels into and from the gill base indicate that they vascularize the gills. Some hint of their fate is offered by Peters (1875) and Wiedersheim (1879), who mentioned scars of one or two blood vessels in the epidermis, once connected to the aortic arch of each side.

A relatively large outpocketing of connective tissue into the head epithelium is located on the side of the head above the gill in *Gymnopis*. The structure is also present in a gill-less 80-mm. embryo that has thickened head epidermis with the connective tissue reduced to a thin layer between epidermis and head musculature. Apparently the "flap" does not act as an operculum or structure later enclosing the gill. A mass of connective tissue is present at the area of previous gill attachment in the oviducal 80-mm. specimen; the mass forms a conspicuous external bulge on the side of the head. At birth, usually 100 mm. or greater in length (Taylor, 1955), there is no evidence of gills, the connective tissue mass, nor the more dorsal connective tissue outpocketing.

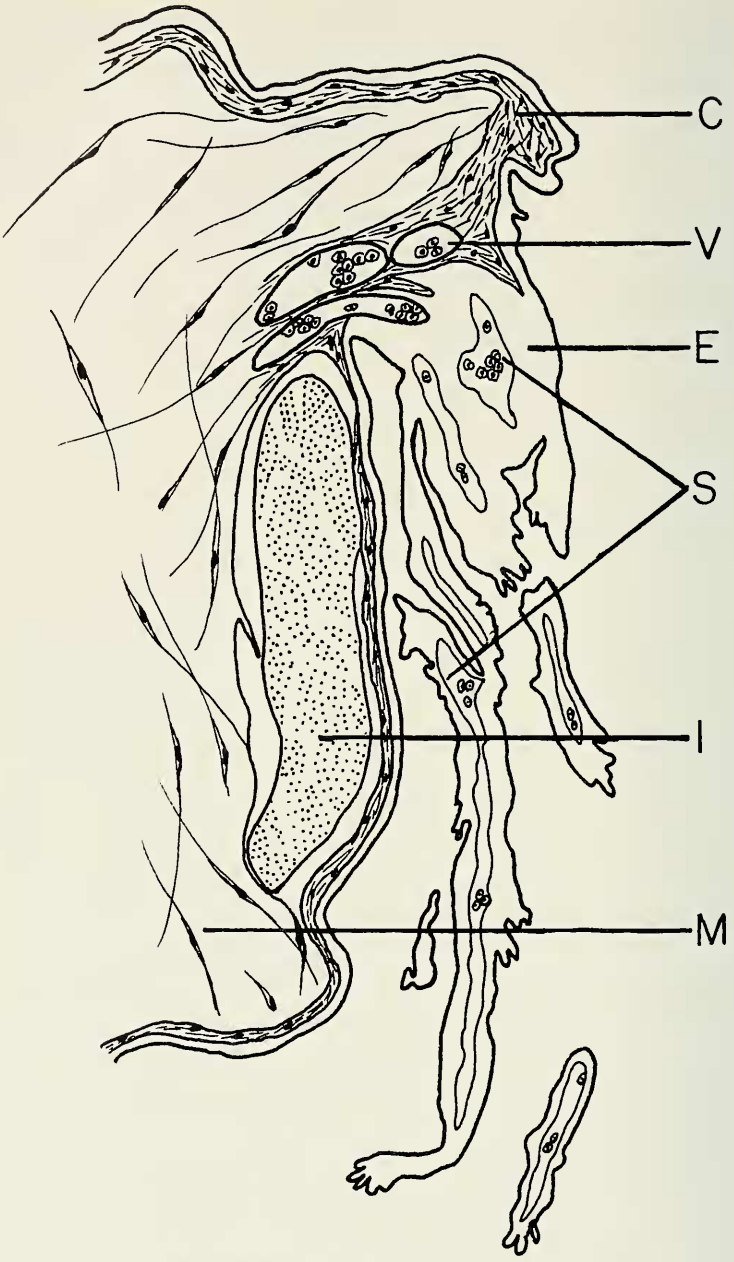


*Figure 2.* Transverse section through right gill of 5.4-mm. *Gymnopis* embryo. 85 x. C=connective tissue; E=epithelium; I=interhyoideus muscle; M=mesenchyme; S=gill sinus; V=vascular arch. Line = 1 mm.

*Discussion*: Published reports on the development of caecilian gills treat primarily the Old World genera *Ichthyophis* and *Hypogeophis*. Müller (1835) reported the occurrence of gills on an *Ichthyophis glutinosus* larva, and the Sarasins (1887-90) briefly discussed the morphology of *Ichthyophis* gills. They reported that the gills are vascularized layers of connective tissue outlined by epithelium. Gill slits are open, and cartilaginous support (a visceral arch) is present for each of the three layers. Brauer (1899) studied the external anatomy of the developmental sequence of two species of *Hypogeophis*. He described the development of triramous, filamented gills from three knobs on each side of the head of the embryo. In a detailed discussion of the development of the visceral clefts and pouches, and their derivatives, Marcus (1908) reported on the external morphology and histology of the gills of *Hypogeophis rostratus*. He thoroughly discussed the relationships of the primary germ layers to gill development, traced development from button-like processes on the outer side of the visceral arches, and analyzed the cellular structure of the gills at each stage of development. Marcus stated that the gill filaments form in sequence, proximal to distal, as outpocketings of the gill tissue. He considered the vascular pattern to be one of loops from the aortic arches; the loops anastomose as development proceeds. Marcus also analyzed the pattern of gill degeneration and loss.

The gills of *Gymnopis multiplicata proxima* described above are at a late stage in development. Degeneration of the gill structure is apparent, and the gills probably would have been lost very shortly. It has long been assumed that caecilian gills are resorbed by the embryo or larva (Sarasins, 1887-90; Brauer, 1899; Parker and Dunn, 1964). Marcus (1908) commented on his initial doubt of the Sarasins' idea of gill resorption (p. 716), but then claims to be able to confirm Sarasins' and Brauer's suppositions that the gills are resorbed. The *Gymnopis* material is apparently very near the last stage of gill degeneration reported by Marcus in *Hypogeophis*. The *Gymnopis* gill agrees in having joined terminal filaments, evidence to Marcus of the "youngest" filaments being the first to undergo a regressive metamorphosis; the structure of the "formed elements" is becoming indistinct; blood cells are found in stages of degeneration; once distinct blood vessels have anastomosed, probably contributing to the formation of the sinuses. Marcus stated that he could not carry the process further but that it was absolutely sure: the gills are not stripped, but resorbed. My material seems to agree quite closely with

Marcus' last reported stage. In this material the left gill of the specimen examined in microscopic section is held to the head only by a long single anterior strand of epithelium. This condition was first observed as the embryo lay undisturbed in the oviduct. The remaining gill structure distal to the strand is in the same state of degeneration as that listed above. However, the epithelium of the posterior part of the head almost covers the original attachment point of the gill. The gill, then, might fall off upon completion of the epithelial layer beneath it. The Sarasins observed in gill-less embryos "sprouts" that they thought were internal gills, but that Marcus considered to be rudiments of the points of origin of the external gill rami. These are present in the 54-mm. gill-less *Gymnopis* embryo. Their presence cannot be considered evidence regarding means of gill loss, since they might remain however the gills are lost. The evidence presented by Marcus and my own observations favor the hypothesis but do not conclusively prove that caecilian gills are reabsorbed. It remains possible that the gill, at least in *Gymnopis m. proxima*, is sloughed off.

Attempts have been made to correlate gill structure with the evolutionary pattern in caecilians by Parker (1956), who discussed the significance of the presence of a deciduous fetal dentition, the type of gill structure, and other features. He found that the specialized dentition occurs only in viviparous (*i.e.*, live-bearing) genera in both the New and Old World. In attempting to correlate this feature with other characters, Parker noted that if the dentition is representative of a natural phylogenetic assemblage, it cuts across systematic arrangements based on other characters. According to Parker, the gills of American caecilians are single and plate-like (see also Parker and Wettstein, 1929, on *Chthonerpeton* and Peters, 1874, 1875, and the Sarasins, 1887-90, on *Typhlonectes*) and those of the African caecilians are triaxial and plumose. It must be assumed that he referred only to the genera known to be viviparous, since the embryos of the oviparous New World genera *Rhinatrema* (Noble, 1927) and *Siphonops* (Goeldi, 1899) had been figured earlier with triramus, filamented gills. The genus *Gymnopis* is live bearing, has a deciduous fetal dentition, *and* has triramous, plumose gills like those of the Old World genera. If, as is usually assumed, the New World and Old World caecilians each form a separate cluster of related genera that is only distantly related to the members of the other geographic unit, the gill structure does not seem to be of particular value in interpreting phylogeny.

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Literature Cited

COCHRAN, DORIS
1961. *The amphibians of the world.* Garden City, New York: Doubleday & Co., Inc., 99 p.

DUNN, E. R.
1942. The American caecilians. *Bull. Mus. Comp. Zool., Harvard Coll.*, 91 (6): 439-540.

GOELDI, E.A.
1899. Uber die Entwicklung von *Siphonops annulatus. Zoologische Jahrbücher Systematik*, 12: 170-173.

MARCUS, H.
1908. Beitrage zur Kenntnis der Gymnophionen. I. Uber das Schlundspaltengebeit. *Archiv für mikroskopische Anat.*, 71: 695-744.

MULLER, J.
1835 Uber die Keimenlocher der jungen *Caecilia hypocyanea. Archiv für Anatomie, Physiologie und wissenschaftliche Medicin*, 1835: 391-397.

NOBLE, G. K.
1927. The value of life history data in the study of the evolution of the Amphibia. *Ann. N.Y. Acad. Sci.*, 30: 31-128.

PARKER, H. W.
1934. Reptiles and amphibians from southern Ecuador. *Ann. Mag. Nat. Hist.*, 10 (14): 264-273.

1956. Viviparous caecilians and amphibian phylogeny. *Nature*, 178: 250-252.

and E. R. DUNN
1964. Dentitional metamorphosis in the Amphibia. *Copeia*, 1964 (1): 75-86.

and O. WETTSTEIN
1929. A new caecilian from southern Brazil. *Ann. Mag. Nat. Hist.*, 10 (4): 594-596.

PETERS, W.
1874. Uber die Entwicklung der Caecilien und besonders der *Caecilia compressicauda. Monatsberichte Akademie der Wissenschaften, Berlin*, 1874: 45-49.

1875. Uber die Entwicklung der Caecilien. *Monatsberichte Akademie der Wissenschaften, Berlin*, 1875: 483-486.

SARASIN, P. and F.
1887-1890. Entwicklung über Anatomie des *Ichthyophis. In Ergebnisse naturwissenschaftlicher Forschungen auf Ceylon*, vol. 4: 153-263.

TAYLOR, E. H.
1955. Additions to the known herpetological fauna of Costa Rica with comments on other species. *Univ. Kansas Sci. Bull.*, 37 (13): 499-575.

TSCHUDI, J. J.
1845. Reptilium conspectus quae in Republica Peruana reperiuntur et pleraque observata vel collecta sunt in itinere a Dr. J. J. de Tschudi. *Archiv für Naturgeschichte*, 11: 149-170.

WIEDERSHEIM, R.
1879. *Die Anatomie der Gymnophionen.* Jena: Verlag von Gustav Fischer, i-vii, 1-101; 9 plates.